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Forest structure and biodiversity in northern boreal forests: Effects of regeneration cutting on flying beetles and wood-decomposing fungi

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ABSTRACT

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The species compositions of flying beetles (Coleoptera) and wood-decomposing fungi (Polyporacea) were studied in relation to the forest structure in the old-growth and managed stands in the northern boreal forests. Coarse woody debris (CWD) turned out be an important component for biodiversity in the old-growth forests. Over half the trapped beetle species were saproxylics, and the polypore diversity was high. Both CWD volume and beetle species richness followed the fertility gradient of the forest site type in the old-growth stands. Deciduous CWD and large-diameter logs at stages of late decay were of special importance for polypore diversity. Of the studied regeneration methods, clear-cuts provided the lowest volume of CWD. Recruitment of new CWD was very low at 15 and 40-year old seed-tree and clear-cut sites, but was maintained at the level of old-growth stands in the new type of selective cuttings. The lack of suitable substrate seemed to be the primary reason for the absence of many saproxylic species from the regeneration areas. Logging waste was able to host only half of the total polypore diversity of seed-tree cut pine forests, and the harvest of large-diameter trunks had significantly decreased the species diversity of polypores in the old selectively logged areas. The results indicate that local extinctions of saproxylic species are probable in the old regeneration areas, where CWD recruitment is low. However, the CWD from the pre-logging period hosted many old-growth forest polypores in the seed-tree cut pine forests several decades after logging, and several groups of saproxylic beetles seemed to be able to live in regeneration areas, provided that suitable substrate was available. Leaving CWD and retention trees of varied sizes and tree species in the managed stands would evidently promote the survival of these species. Both the beetle and polypore species in spruce forests seemed to be more sensitive to logging than the species in pine forests. The numbers of fungus-living and rare beetles were distinctly lower in the clear-cuts than in the old-growth spruce forests. Also some polypore species, especially those confined

to large-diameter trunks and late decay stages, seemed to be sensitive to loggings. Maintaining populations of these species groups may turn out to be difficult or impossible at regeneration sites.

Key words: biodiversity, boreal forests, Coleoptera, Polyporaceae, decaying wood, saproxylic species, regeneration cutting

LIST OF ORIGINAL PAPERS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I Sippola, A-L., Siitonen, J. and Kallio, R. 1998. Amount and Quality of Coarse Woody Debris in Natural and Managed Coniferous Forests near the Timberline in Finnish Lapland. Scandinavian Journal of Forest Research 13:204-214.

II Sippola, A-L., Siitonen, J. and Kallio, R. 1995. Faunistics of Coleoptera in subarctic pine forests in Finnish Lapland. Entomologica Fennica 6:201-210.

III Sippola, A-L., Siitonen, J. and Punttila, P. 2002. Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland. Annales Zoologici Fennici 39 (in press).

IV Sippola, A-L. and Renvall, P. 1999. Wood-decomposing fungi and seed-tree cutting: A 40-year perspective. Forest Ecology and Management 115:183-201.

V Sippola, A-L., Lehesvirta, T. and Renvall, P. 2001. Effects of selective logging on coarse woody debris and diversity of wood-inhabiting fungi in eastern Finland. Ecological Bulletins 49:243-254.

CONTENTS

CONTRIBUTIONS

The following table shows the major contributions of authors to the original articles.

	I	II	III	IV	V
Original idea	JS, ALS	ALS, JS	ALS, JS	ALS	ALS
Study design	JS, ALS	ALS, JS	ALS, JS	ALS	ALS
Empirical data gathering	RK, ALS	RK, ALS	ALS	ALS, PR	TL, ALS
Identification of species	-	JS	JS	PR	TL, PR
Data analysis	RK, ALS	RK, ALS, JS	PP, ALS, JS	ALS	ALS, TL
Manuscript preparation	ALS, JS, RK	ALS, JS, RK	ALS, JS, PP	ALS, PR	ALS, PR, TL

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1. INTRODUCTION

The main part of Fennoscandia belongs to the boreal forest zone, which is dominated by two coniferous tree species: Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) (Ahti et al. 1968). Over 80 % of the above-ground biomass in the northern boreal forests can be bound in the trees (Havas and Kubin 1983). In the natural state, the processes that modify the structure of forests are the death of trees by small-scaled gap dynamics or large-scale exogenous disturbances, decomposition, i.e. the liberation of nutrients from organic material, and regeneration where a large proportion of nutrients are again bound to woody material.

The death of single trees creates free space for new seedlings, allowing the regeneration of forest. In boreal spruce forests, injuries and tree deaths are commonly caused by insects and fungi (Sirén 1955, Norokorpi 1979). Mammals, including elk, reindeer, mountain hare, and voles often damage or kill saplings. Flooding, land slides, wind and a heavy snow load are among the physical factors that can cause small or medium size gap formation within stands, the latter two often snapping or tumbling trees that are weakened by insects or fungi (Cajander 1917, Syrjänen et al. 1994, Kuuluvainen et al. 1998). Large-scaled natural disturbances in boreal forests are caused by either fire or storms (Bonan and Shugart 1989, Kuuluvainen 1994). Fire has been a relatively regular disturbance factor in dry forest site types, occurring, for instance, in the northern boreal lichen-*Calluna*-type forests in Sweden on average between 50 and 120 years (Zackrisson 1977, Engelmark 1984). Fires in dry sites have often been of low intensity, creating small-scale vegetation mosaics (Syrjänen et al. 1994). In mesic and moist boreal forests, the interval between fires has varied, according to the forest site type and region, from 90 to 500 years (Zackrisson 1977, Foster 1983), and in wet places, the role of wildfire has probably been negligible (Syrjänen et al. 1994). Storms are an irregular but essential disturbance factor in boreal forests. In mesic spruce stands, wind is the most important exogenous disturbance, commonly creating patches of 0.01-0.5 ha into the forest (Syrjänen et al. 1994). Large-scale windthrows are more rare, but not exceptional at the regional level. For instance, in the 1980s five major storms occurred in Finnish Lapland, each felling 0.2-3 million cubic meters of timber (Saarenmaa 1989).

When a tree or a part of it dies, a variety of decaying wood is formed, including standing dead trees and snags, logs, chunks of wood, branches,

stumps and roots. The relatively large pieces of decomposing wood collectively are called coarse woody debris (CWD) (Harmon et al. 1986). The minimum diameter of CWD varies in different studies, but is usually from 2.5 to 7 cm (Harmon et al. 1986). The nutrients are mainly liberated from CWD by invertebrates, fungi, and bacteria (Rayner and Boddy 1988a, b, Speight 1989). Although CWD may be a nutrient sink in the short run, it can be a major long-term source of nutrients in many ecosystems (see, e.g., Larsen et al. 1978, McFee and Stone 1966). "Nurse logs", i.e. decomposing trunks of fallen trees, are found to serve as a regeneration base of seedlings in many forest types (Harmon et al. 1986), for instance in mesic boreal spruce forests (Arnborg 1943).

CWD serves as a habitat for many species. Snags and logs are important for cavity nesters, in boreal forests especially for hole-nesting bird species (Samuelsson et al. 1994). A large variety of invertebrates, mosses, lichens, fungi, and bacteria inhabit decaying wood (Esseen et al. 1992, Samuelsson et al. 1994). Invertebrate species that are dependent during a part of their life cycle upon dead or dying trees or pieces of trees, or upon wood-inhabiting fungi, are called saproxylic species (Speight 1989). In addition, the species that are dependent upon the presence of other saproxylic invertebrates fall into this category. Among fungi, the species utilizing non-living organic material, other than those killed by the fungus itself, are called saprotrophic (Cooke and Rayner 1984). Most wood-living fungi are saprotrophic, even though some of them are necrotrophic; first killing the tree and then utilizing it as a resource. Later in this thesis, both saprotrophic and necro-saprotrophic fungi, and saproxylic beetles are called saproxylics.

The forest gap dynamics at a stand level is stochastic, and, consequently, the occurrence of CWD within a forest stand is uneven, creating a patchy and temporally limited resource for saproxylic species (Esseen et al. 1992). Several different factors affect the survival of populations at the stand level. The temporal variation of substrate has to be sufficiently frequent, i.e., the continuity of CWD must be ensured, and the spatial variation of suitable microhabitats affects the possibilities of a species to disperse to the new substrate (Speight 1989). The decay process of a tree follows a successional pattern, where primary colonizers are followed by secondary species. These successional stages are characteristic for each tree species, but the faunal and floral composition can also vary considerably within the same tree species, depending on several factors such as the decay stage, trunk diameter, the microclimate, the chemical composition of wood etc. (Swift 1987, Rayner

and Boddy 1988 a, b; Speight 1989, Boddy 1992). Within a trunk, the colonization order and interspecific relations of species within the wood affect the species composition of wood-decomposing fungi (Niemelä et al. 1995, Renvall 1995). Interspecific competition can affect the survival of decomposer species particularly in the paucity of substrate, since some species are stronger competitors than others are (Rayner and Boddy 1988a, Holmer 1996).

Large-scale utilization of forests for industrial purposes has operated about 150 years in Fennoscandia (Östlund 1993), changing and modifying the structure and processes of forests (Esseen et al. 1992). The main effects of forestry have been the fragmentation of earlier large continuous forest areas, the decrease in the area of old-growth forests, even-aged stand structure, the decrease in the number of deciduous trees and in the volume of decaying wood, and changes in disturbance dynamics, such as the elimination of forest fires (Berg et al. 1994, Angelstam 1996, Esseen et al. 1997). During the past decades, the decrease in the diversity of many forest-dwelling species groups has became obvious. Invertebrates and lower plants have especially been affected (Rassi et al. 1992, Ehnström et al. 1993). The large number of endangered saproxylic and saprotrophic species in Fennoscandia (see Rassi et al. 1992, Ehnström et al. 1993) indicates that the environments created by modern forestry have not fulfilled the habitat requirements of a large portion of saproxylic species. Of the approximately 3 600 beetle species known from Finland (Silfverberg 1992) about 800 are saproxylic (Siitonen 1998). The number of threatened beetles totals 332, and 39 % of them are considered to be threatened because of the decrease in the amount of decaying wood (Rassi et al. 1992). The number of polyporous fungi in Finland is 212 (T. Niemelä 1999), 61 of which are regarded as threatened or rare (Kotiranta and Niemelä 1996). Because the majority of polypores are wood-decomposing fungi, forestry operations, which have affected the amount and quality of CWD, are the main reasons for their rarity (Rassi et al. 1992).

Finland has ratified the United Nations' Convention on Biological Diversity, which obliges the participants to protect biological diversity in their countries (Ympäristöministeriö 1993). The Forestry Law of Finland aims at fulfilling the goal of the convention by stating that biological diversity should be protected in forestry operations (Suomen Säädöskokoelma 1093/1996). To be able to protect species diversity within different forest site types we should know what kind of species assemblages are typical for

natural forests, which structures and processes are essential in maintaining the diversity of different organism groups, and how these features can be preserved in practical forestry operations. Our knowledge is still scarce, for instance, on the variation of the amount and quality of CWD in different forest site types of old-growth forests and on the influence of different forest management methods on this resource. In addition, our knowledge on the composition of invertebrate and fungal communities in northern boreal forests is incomplete.

Forestry has operated in the timberline forests of Finland for only a few decades (Veijola 1998), and the regeneration cuttings of pristine forests provide the opportunity to follow the changes that forest management cause in the composition of the flora and fauna. The large natural forests of northern nature conservation and wilderness areas offer good reference sites for the stands altered by modern forestry. In this thesis I have studied the species composition of flying beetles (Coleoptera) and wood-decomposing fungi (Polyporacea) in relation to the forest structure, and especially to CWD, in old-growth and managed stands in the northern boreal forest zone both in the northernmost part of the zone near the timberline and in the southernmost part of the zone. More specifically, the aims of this thesis have been:

(1) to study the amount and quality of CWD in different forest site types of old-growth stands, and to examine how different forest regeneration methods affect the volume and quality of CWD (paper I),
(2) to study the composition of beetle and polypore assemblages in old-growth forests in relation to forest structure and CWD (papers II, III, IV, and V), and
(3) to study the effects of regeneration cutting on beetle fauna and wood-decomposing fungi (papers III, IV, and V).

2. MATERIALS AND METHODS

2.1. Study areas and sites

The study was conducted in northern Finland in the provinces of Lapland and Kainuu. In both regions, the study areas represent northern boreal forest zone (*sensu* Ahti et al. 1968). The areas in Lapland are located in the northernmost part of the zone and the areas in northern Kainuu in the southernmost part of the zone.

In Lapland, six separate study areas (Fig. 1) were chosen between the latitudes 68°N 24°E - 68°45´N 28°25' E (I). The study areas 1-3 comprised of forests dominated by both Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.), whereas the areas 4-6 were located north to the northern timberline of spruce, and comprised only of pine forests. Altogether, 46 study sites were established in the six areas. The size of each study site was 1 ha, except in 12 sites, where the size was 0.5 ha because the terrain restricted the establishment of 1 ha quadrate plots. The sites located 150-350 m a.s.l.

The sites in the old-growth forests represented three main forest site types of the region: (1) pine-dominated, (2) spruce-dominated, and (3) herb-rich mixed forest site types. Both in pine and in spruce forests, pubescent birch (*Betula pubescens* Ehrh.) was found as an admixture tree. The mixed forests were dominated by spruce with admixtures of birch, aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.), goat willow (*Salix caprea* L.), and bird-cherry (*Prunus padus* L.). The overall number of replicates in the four studies conducted in Lapland (I-IV) was 21 in pine-dominated forests, 6 in spruce-dominated forests, and 4 in herb-rich mixed forests (see Table 1).

In the regeneration areas of Lapland, the sites represented different forest types as follows:

(4) Recent (1-3 years ago) seed-tree cut pine forests, where the seed trees remained unlogged. The number of seed-trees was 80-120 per hectare.
(5) 15-18 year-old seed-tree cut pine forests where the seed-trees had been removed. The mean height of saplings at the sites was 3.5 m.
(6) Approximately 40 year-old seed-tree cut pine forests where the young forest was growing. The mean height of saplings at the sites was 7.4 m.

(7) 15-year old clear-cuts of spruce forests, where the soil has prepared by ploughing and which had been planted with pine. The mean height of the saplings was 3.4 m.
(8) 2-year old selective cuttings of pine forests. In this method, the naturally uneven age structure of forest is maintained during logging (Metsähallitus 1992). Mature trees were cut in the places where a sapling stand had been established, but all the growing trees were left as well as seed trees in the places with insufficient sapling growth (I).

Each treatment and age group was represented by three replicates.

The amount and quality of coarse woody debris were studied in all the six study areas (I). The relationships between forest structure features and beetle fauna were studied in the areas 1-5 (II and III), and the effects of forest management on wood-rotting fungi in the areas 3 and 5 (IV) (Fig. 1).

The effects of old selective logging on the diversity of wood-inhabiting fungi were studied in Kainuu, where ten study sites were established in two areas between the latitudes 64°N 27°E - 65°N 28°E (V) (areas 7-8, Fig. 1). The sites located 255-355 m a.s.l. All the stands represented mesic spruce forests, with admixture of birch, aspen, rowan, and goat willow. In the Metsäkylä sites (area 7), some amount of Scots pine occurred as admixture. Five of the stands were primeval forests that had never been subjected to logging, while five were selectively logged between 1894 and 1942 (V). In each stand, the study was conducted in two 150 m long transects, where five circular sample plots were established in 50 m intervals, making a total of ten plots per each study site. The radius of the plots was 20 m in CWD measurements, and 10 m in the polypore research (V).

Selective logging was a common logging method in Finland at the end of the 19th and beginning of the 20th century. When using this method, trees that exceeded a certain minimum diameter at a given height were removed. The minimum diameter of logged trees varied at different times as well as according to the use of timber (Karjalainen 1998). It was possible to date back from the forest history documents the time of the logging and the main quality and size of logged timber at the logged areas, but because the forest documents from that time usually concern relatively large areas, it was not possible to date back exactly the number of removed trees per site. To get information on the intensity of logging at the sites, the number of cut stumps per hectare was counted (V). Both the forest history documents

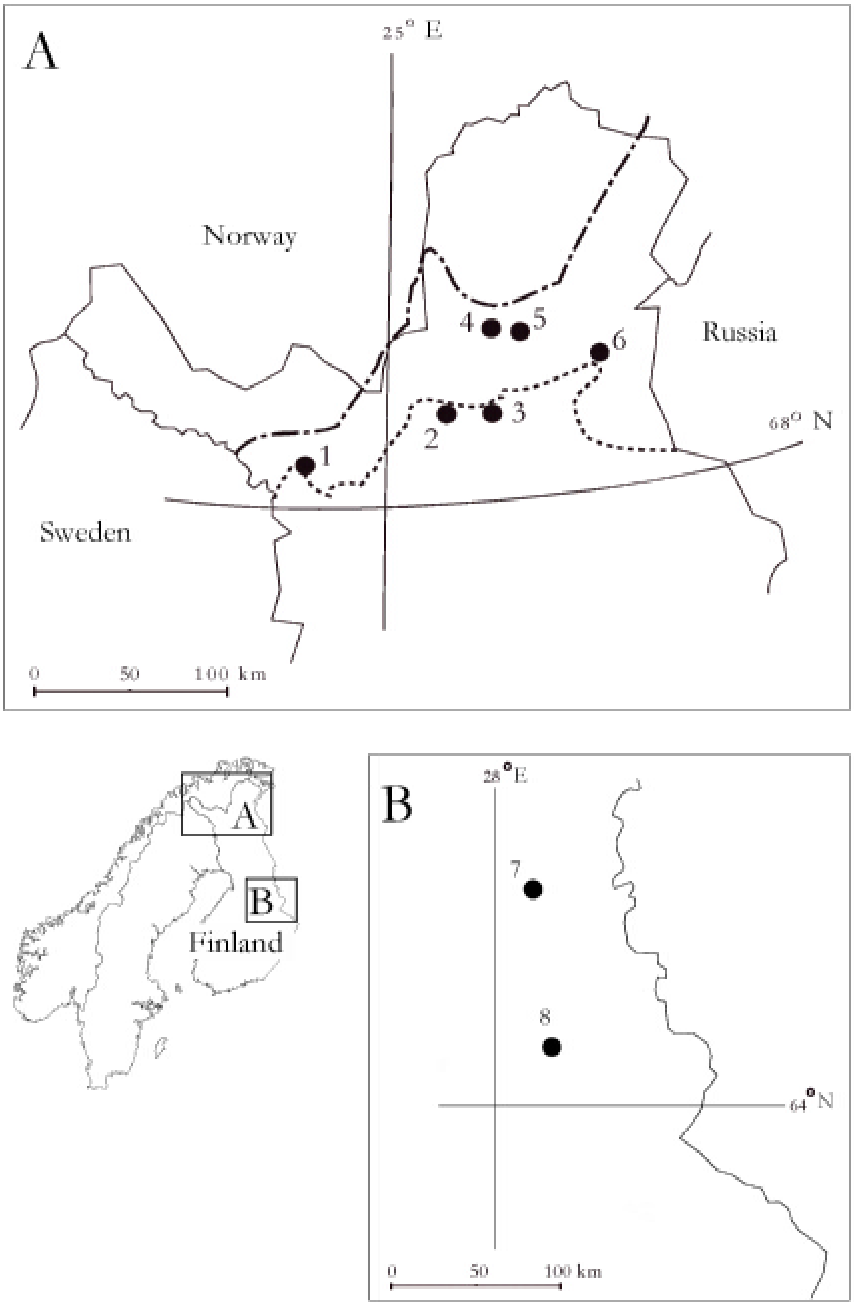

Figure 1. Location of the study areas in Lapland (A) and Kainuu (B). 1 = Pallas-Ounastunturi, 2 = Härkäselkä, 3 = Sotajoki, 4 = Vaskojoki, 5 = Nukkumajoki, 6 = Pitkäjärvi, 7 = Metsäkylä, 8 = Paljakka. The nothern limit of spruce forest is indicated by the lower and that of pine forest with upper dashed line in the Fig. A.

Table 1. Forest categories, study areas, numbers of replicates and comparisons between forest categories in different studies. For the study areas, see Fig.1. [1)] Data included to the data of old-growth pine forests. [2)] Not included to the data of old-growth spruce forests. [3)] Includes one site which is not included in the data in paper I.

Study	Forest categories	Study areas	No. of replicates	Comparisons
CWD studies (papers I, V)	**Old-growth forests**			
	Pine	1-6	20	Old-growth forest categories among each other
	Pine, pre-logging data of 1-yr. old seed-tree cut sites	5	3 [1)]	
	Pine, controls for 2-yr. old selectively cut site	6	3 [1)]	
	Spruce	1,3	5	
	Spruce, controls for old selectively cut sites (60-100 yr.)	7,8	5 [2)]	
	Herb-rich, mixed	1,3	4	
	Seed-tree cut pine forests			
	1-yr. old	5	3	1-yr. old seed-tree cut sites with pre-logging data
	15-yr. old	3	3	15- and 40-yr. old seed-tree cut sites with old-growth pine forests
	40-yr. old	3	3	
	Clear-cut spruce forests, planted with pine			
	15-yr. old	1	3	Clear-cut sites with old-growth spruce forests
	Selectively cut pine forest			
	2-yr. old	6	3	2-yr. old selectively cut sites with control sites
	Selectively cut spruce forests			
	60-100-yr. old	7,8	5	Selectively cut spruce forests (60-100 yr.) with control sites

Beetle studies (papers II, III)	**Old-growth forests**			
	Pine	1-5	9 [3)]	Old-growth pine forest data in 1992 and 1993
	Spruce	1,3	6 [3)]	Old-growth forest categories among each other
	Herb-rich, mixed	1,3	4	Old-growth forest categories among each other
	Seed-tree cut pine forests			
	1-yr. old	5	3	1- and 15-yr. old seed-tree cut areas with old-growth pine forest
	15-yr. old	3	3	
	Clear-cut spruce forests, planted with pine			
	15-yr. old	1	3	15-yr. old clear-cut sites with old-growth spruce forests
Polypore studies (papers IV, V)	**Old-growth forests**			
	Pine	3,5	4	
	Spruce	7,8	5	
	Seed-tree cut pine forests			
	3-yr. old	5	2	3-, 18-, and 42-yr. old seed-tree cut sites with old-growth pine forests
	18-yr. old	3	2	
	42-yr. old	3	2	
	Selectively cut spruce forests			
	60-100-yr. old	7,8	5	60-100-yr. old selectively cut sites with old-growth spruce forests

and the number of cut stumps revealed that the logging intensity had varied considerably between the sites (V).

2.2. Measurement of environmental variables and coarse woody debris

Environmental variables of the study sites were examined in order to detect the amount and quality of CWD, and to study the relationships between forest structure and the composition of beetle fauna and polypore flora. The volume of living timber and the amount and quality of CWD were studied at all the sites (I, V; the data of paper I was used in the studies II, III and IV). In addition, the composition of understorey vegetation cover, the percentage coverage of bushes and litter, and the thickness of humus layer were studied at the beetle study sites (III).

Living trees were measured by tree species in five (I) or ten (V) relascope plots at each study site, depending on the study design. In the sapling stands, the saplings were measured on ten circular plots of 50 m^2 (radius = 3.99 m).

All coarse woody debris with a minimum diameter of 1 cm at breast height (DBH = 1.3 m) (entire trees), or with a minimum length of 1 m and mid-diameter of 5 cm (snags, logs, branches and stumps) were measured and recorded into one of the following categories: (1) logs, (2) snags (standing dead trees and broken-top snags) (3) branches, (4) natural stumps, (5) cut stumps, (6) cut butts, and (7) logging waste (incl. cut branches and tree-tops). Five different decay stages were distinguished:

1 = 1-2 years from death, bark and phloem still fresh. Knife penetrates only a few mm into the wood.
2 = wood hard, most of the bark left in conifers, but no fresh phloem. Knife penetrates 1-2 cm into the wood.
3 = wood partly decayed from the surface or in the centre (depending on tree species), usually at least part of the bark loosened or detached in conifers. Knife penetrates 3-5 cm into the wood.
4 = most of the wood soft throughout, usually no bark left on conifers. The entire blade of the knife penetrates easily into the wood.
5 = wood almost completely decomposed and disintegrating when removed, forest-floor mosses and lichens covering the trunk.

The composition of plant cover of the field and the bottom layers were studied in ten 1m^2 squares in each beetle study site by using percentage coverage estimation with the intervals + (<1 %), 1, 3, 5, 7, 10, 15, 20, 25....100 % (III). Vascular plants were identified to the species level. The groups *Cladonia uncialis* coll., *Stereocaulon* sp., *Sphagnum* sp. and Hepaticae coll. were used in the identification of lichens and mosses; otherwise the species were identified to the species level. For the analyses, vascular plants were grouped into four groups, indicating oligotrophy, mesotrophy, eutrophy, and moisture. The grouping of plants was based on Kalela (1961), Kaakinen (1982), and Eurola and Virtanen (1989). The thickness of the humus layer was measured using three classes (< 2 cm, 2-5 cm and > 5 cm).

2.3. Sampling of beetles

The composition of beetle fauna in old-growth pine forests was studied in the summer 1992 (II). To detect variation in the species composition among the forest site types in old-growth forests, and the effects of forest management on species diversity, another sampling was conducted in 1993 (III). This study comprised old-growth pine, spruce, and mixed forests, 1- and 15-year-old seed-tree cut sites, and 15-year old clear-cut sites. The species compositions of different types of old-growth forests were compared with each other, and the species compositions of regeneration areas were compared with the respective types of old-growth forests (i.e., seed-tree cut pine forest with old-growth pine forests and clear-cut spruce forests with old-growth spruce forests; see Table 1).

Window flight traps were used to collect beetle data. The traps in 1992 were composed of acrylic windows with open flowerpots as sampling vessels, and they were hanging about 1.2-1.7 m above the ground. Because the open, salt-containing pots attracted reindeer, they were replaced by bottles in 1993. In 1992, two traps were used pairwise in the middle and opposite corners of the sites, making a total of six traps at 6 sites, while at 6 sites only one pair of traps was used in the middle of the site to compare the efficiency of this trapping effort. In 1993, 5 traps were used, one in the each corner and one in the middle of the study sites. The sampling was conducted from the beginning of June until mid-September in both years.

Window flight traps do not catch non-flying species living in soil or undergrowth vegetation. Because the traps are usually hanging 1,2 - 1,7 m

above the ground, also species flying very low may avoid the traps. Empirical data shows, however, that window flight traps catch about 60 % of the beetle fauna of forests (Similä et al. 2001), giving thus a relatively good overview of the coleopteran fauna. The method is widely used because it gives large samples with a relatively small trapping effort, and standardized trapping makes it possible to compare species compositions of different habitats. Compared with other trapping methods (trunk-window traps, extraction cylinders, pitfalls, and bark peeling and other manual methods) window flight trapping yields the largest number of species, and gives a relatively good picture of saproxylic species (Siitonen 1994, Økland 1996, Similä et al. 2001). Økland (1996) estimates that the method is better suited for comparisons of beetle assemblages between different forest environments than trunk-window traps, but it collects lower number of rare and threatened species than the latter method (Muona 1999, Martikainen 2000).

2.4. Investigation of wood-decomposing fungi

To study the effects on seed-tree cutting on wood-decomposing fungi, a survey was conducted in the old-growth pine forests and differently aged (3, 18, and 42 -year-old) seed-tree cut sites in Inari Lapland in August, 1996 (IV). The sample plots were located inside the 1-hectare sites used in the CWD and beetle studies. The size of each plot was 3000 m^2. All parts of dead wood with a minimum base diameter of 10 cm were studied in the plots. The main decayers, including polypores and large corticioid species, and sporocarps of lignicolous hydnoid fungi were included into the survey.

The effects of the selective logging of spruce forests on the polypore flora were studied in August-September in 1997 and 1998 in Kainuu. The species composition of the sites that had been selectively logged with different intensity 60-100 years ago were compared with the species composition of the primeval forests sites that had never been subjected to forestry (Table 1). The study was conducted in ten circular plots with a radius of 10 m at each site, making a total survey area of 3140 m^2 per site per year (V). The polyporous fungi were recorded on all the CWD with a minimum length of 1 m and minimum base diameter of 5 cm.

2.5. Data analysis

The number of species per study site or area was used as a measure of species richness among the forest site types and treatments. In natural environments, the sampling effort affects the number of observed species: the species number grows with the increasing number of observations until all the species of the study area are included. Because it is unlikely to get the total species number sampled in natural communities especially in the case of invertebrates, where the majority of species are relatively infrequent (May 1975), the comparison of different sample sizes may give misleading results. However, originally different sample sizes can be compared by using rarefaction. With this method, the expected numbers of species can be calculated for the subsamples that have been randomly drawn from the original data. Drawing successively smaller subsamples, rarefaction curves with the expected species numbers for given sample sizes can be drawn (Simberloff 1978, James and Rathbun 1981), which enables the comparison of expected species richness for a given sample size. However, the sample size cannot be larger than the number of individuals (or observations) in the smallest sample. Statistical differences can be examined by drawing segments of ±2 standard deviation lines for a determined number of observations, which show the 95 % confidence limits for the expected species number, thus enabling direct observations on the statistical differences (Tipper 1979). Rarefaction was used in comparing beetle species richness in papers II and III. In paper II, the statistical difference was examined from the rarefaction curves of the pooled samples of the study areas. In paper III, the expected species numbers for a given sample size of each study site were tested using the Mann-Whitney U-test and the Kruskall-Wallis one-way analysis of variance, with *a posteriori* comparisons of mean ranks in comparison of the median numbers of species among the stand categories. Rarefaction was used also in comparing the species richness of polypores between the pooled catches of different forest categories in the Inari area (IV), where statistical testing was problematic due to the low number of replicates. Otherwise, the comparisons of species data were made with Mann-Whitney U test (II, V) or Kruskall-Wallis test (II, V), because the species data were not normally distributed.

Unlike species richness, diversity indices take into account the species abundances (Magurran 1988). Fisher's alpha diversity index (Fisher et al. 1943) was used to compare the diversity of beetles in pine forests (II) and

the diversity of wood-decomposing fungi between controls and treatments (IV, V). The index is commonly used in entomological studies, because the numbers of individuals representing different species have found to follow a logarithmic series in many insects populations (see Magurran 1988). The advantage of the index is also that it is relatively little affected by sample size, and it is not particularly sensitive to common or rare species (Kempton and Taylor 1974, Magurran 1988), as are some other widely used diversity indices (Peet 1974, Spellerberg 1991).

The similarities in the species compositions were compared with the Sørensen binary index (II) and the Renkonen's percentage similarity index (Renkonen 1938) (II, IV). The Sørensen index only takes into account the presence/absence of a species and is thus independent of the relative abundances of species (Wolda 1981), while the percentage index mostly depends on the relative abundances of abundant species. In paper V, the differences in the similarity indices within and between primeval and logged sites were tested using the one-way analysis of variance, and the Bonferroni test was used in pairwise comparisons.

The differences between environmental variables were tested by either the one-way analysis of variance, using Student-Neuman-Keuls as *a posteriori*-test (I) or Student's T-test (V). The Pearson correlation coefficient was used in the correlation analysis between timber variables (I), and Spearman's coefficient was used in the correlation between the environmental variables and species data (III, IV, V). If the environmental data were large, the risk level in correlation analysis was adjusted with a Bonferroni correction (III, V) (Rice 1989).

Correspondence analysis (Ter Braak and Šmilauer 1998) was used in papers III and IV in order to explore variation in the species composition among the stand categories, and the relations between species composition and environmental variables. The beetle data (III) was $ln\,(x+1)$-transformed. The analyses were conducted separately for saproxylic and non-saproxylic beetle species. In the polypore data (IV), we wanted to examine the effects of logging on pine-living species in particular, and the species growing on deciduous CWD were excluded from the analysis. Ordination analysis is sensitive to rare species (Ter Braak and Prentice 1988), and to avoid their effect in the beetle data (III) only species occurring at more than one site were included in the analysis. In the polypore data, the species with only one representative were excluded from the ordination (IV).

3. RESULTS AND DISCUSSION

3.1. Coarse woody debris

3.1.1. Amount and quality of coarse woody debris in old-growth forests

The main factor that affected the volume of CWD in pristine forests was the volume of living trees (I), which reflects the site productivity. The productivity of a forest stand is mainly determined by climatic and edaphic factors, and the topography (Spurr and Barnes 1973), decreasing by latitude and altitude. In boreal forests, there is a growing gradient in the annual increment within the biogeographical zone from dry, pine-dominated forests to herb-rich, mesic spruce-dominated mixed forest (Cajander 1926, Kalela 1961). The mean volumes of CWD were approximately equal in the old-growth pine and spruce forests (19 m^3 ha^{-1}), where also the mean volumes of living timber where about equal (81 and 85 m^3 ha^{-1}), but they were considerable higher (60 m^3 ha^{-1}) in herb-rich mixed forests, where the mean volume of living timber was almost doubled (152 m^3 ha^{-1}) (I). There was a large variation in the volumes of both living timber and CWD within the old-growth pine forests. This variation is partly explained by the topographic, microclimatic, and edaphic variation between the sites, but may also be partly explained by past disturbances.

The CWD volumes measured in old-growth timberline forests corresponded to 20-30 % of the total timber volume (living and dead) of the stands (I). In the spruce forests of northern Kainuu (64-65° N) at the southern limit of the northern boreal zone the mean volume of CWD was 51 m^3 ha^{-1} (V), representing 16 % of the total timber volume of the stands. Different studies from the boreal zone in Fennoscandia and northern Russia report CWD volumes between 32 and 201 m^3 ha^{-1} in old-growth mesic spruce forests (63-67° N, Siitonen 1994, Linder et al. 1997), and between 60 and 120 m^3 ha^{-1} in old-growth pine forests (62-66° N, Linder 1986, Linder et al. 1997). The volumes decrease considerably by latitude: according to Siitonen (2001), the mean volumes of CWD in the middle and southern boreal forest zones are 60-120 m^3 ha^{-1} in old-growth pine forests, and 90-120 m^3 ha^{-1} in old-growth mesic spruce forests, which are 3-6 times higher than volumes which were measured in timberline forest (I). In addition, the mean volumes measured from the more southern parts of the northern

boreal zone are clearly higher (50-80 m^3 ha^{-1} in spruce and 70 m^3 ha^{-1} in pine forests, Siitonen 2001) than those measured near the timberline (I). However, the proportions of CWD of the total timber volume were similar in the timberline (25-28 %, I) to those measured in the other old-growth forests in Finland (cf. Siitonen 2001). Somewhat higher proportions have been measured in other parts of the boreal zone: in the spruce forests of Komi in northwestern Russia the proportion of CWD was 35-40 % (Kuuluvainen et al. 1998), and the average proportions in both spruce and pine forests in central and northern Sweden amounted 30 % of the total stem volume (Linder et al. 1997). The fact that the proportions of CWD of the total timber volume near the timberline were at the same level as in the other regions provides evidence that the lower decay rate compensates the slower accumulation of CWD in the northern latitudes (cf. Siitonen 2001). Very little information exists on the decay rates of wood in the boreal zone in Fennoscandia, especially near the timberline. However, existing studies show that there is considerable variation in the decay rate between the southern and northern ends of the boreal zone. The minimum time for the complete decay of spruce logs in southern Sweden was 70 years (Liu and Hytteborn 1991), whereas it was 200 years in northern Sweden (Hofgaard 1993).

In addition to stand productivity, the intensity and frequency of disturbances cause variation in CWD volumes both between and within the forest site types. There was a large variation in the volume of CWD especially within timberline pine forests (I), but also among spruce-dominated stands in Kainuu (V). Past fires can be one explanation for the present variation in the CWD volumes. Fire frequency in boreal forests varies according to the tree species composition, stand structure, soil conditions, exposure, topography, and climate (Esseen et al. 1997). Average forest fire frequencies between 50-120 years have been detected in dry pine-dominated forests in northern Sweden, whereas the fire interval in mesic mixed forests has been at least 90 years or more (Zackrisson 1977, Engelmark 1984, 1987). Fire scars were detected at 70 % of the pine-dominated timberline forest sites (I). Even though these fires probably date back at least 80-100 years, their input can still be visible. The amount of CWD created in a wildfire varies greatly depending on the type of fire (ground, surface, or crown fire), its intensity, tree species, and stand structure. According to Harmon et al. (1986), the input of a single fire can be equivalent to centuries of the "normal" annual input of CWD. There were no visible signs of fires or other large-scale exogenous disturbances among the spruce forest sites in Kainuu, and

it is probable that the variations in the CWD volumes are explained by the more fertile soil type in Paljakka (area 8, see Fig. 1) than in Metsäkylä (area 7) (V), and by the differences in the small-scale gap dynamics.

Wind is the most important natural exogenous disturbance factor in the mesic sites of boreal forests (Syrjänen et al. 1994). The amount of windfalls in a stand varies depending on the wind velocity and direction, topography, soil type, and tree species. The volume of CWD in a pine-dominated stand in western Lapland, felled partly by a storm seven years ago, totalled 40 m^3 ha^{-1}, and in a storm-felled spruce-dominated stand of similar age 69 m^3 ha^{-1}, representing 40 % and 56 % of the total timber volumes of the sites (Sippola, unpublished). CWD created yearly by small-scaled gap dynamics varied 2-5 % of the CWD volume of the stands (I, V). Large exogenous disturbance can thus create a 10-20 -fold supply of CWD at a time compared with small-scaled gap dynamics, providing decaying wood for decades, or in dry pine forests, for even a century or more. However, large-scale storms are occasional and stochastic phenomena. At the local level, small-scale gap dynamics is an important factor, especially in mesic and wet sites. The low frequency of large-scale disturbances and the high volume of CWD created by various small-scaled factors provide long forest continuity and a heterogeneous environment for saproxylic organisms at the moist sites (Angelstam 1996). This heterogeneity is increased by increasing tree species diversity in fertile soils. Deciduous CWD is an important factor for the diversity of both invertebrates and wood-decomposing fungi (Ehnström and Walden 1986, Esseen et al. 1992, Kotiranta and Niemelä 1996). With the exception of a few purely pine-growing sites, deciduous CWD, mainly birch, was found in all the forest stands (I, V). In timberline pine forests, it amounted on average to 1-1.5 m^3 ha^{-1}. The volumes increased with the increasing fertility of the forest site type, being on average 6 m^3 ha^{-1} in spruce and 16 m^3 ha^{-1} in herb-rich mixed forests (I). In the spruce forests of Kainuu, the average volume of deciduous CWD amounted 20 m^3 ha^{-1}, but the variation among the sites was large (V). The presence of deciduous CWD markedly increased the species richness of both beetles (III) and wood-decaying fungi (IV, V).

The proportion of logs was 60-80 % of the total volume of CWD in all the forest site types, and the proportion of snags 18-35 % (I, V). Although the main part of the CWD volume is found in logs, it is notable that about one fifth or more of the CWD in the old-growth forests are standing dead trees or snags, which are important for cavity-nesting species.

The volume of entire large-diameter logs (DBH > 30 cm) varied from 14-17 % of the total timber volume in timberline pine and spruce forests (I), whereas their proportion was 36 % in the spruce forests of Kainuu (V), and as high as 51 % in the spruce-dominated mixed forest near the timberline (I). As pointed out in many studies (see e.g., Bader et al. 1995, Økland et al. 1996, Lindblad 1998), large-diameter logs are of special importance for the diversity of a large number of beetles and polyporous fungi.

The proportions of the decay stages reflect the yearly input of CWD, the decay rate, and the time since disturbance. The proportions of the different decay stages of the total timber volume were relatively even between the forest site types in the timberline, except decay stage 2 (I), which represent the supply of CWD on the time scale from two to approximately 15-30 years since the death of a tree. The great variation in the proportion of this decay stage (6-44 % of the total CWD volume (I, V)) demonstrates the stochastic recruitment of CWD, and the fact that many causes of tree mortality exhibit aggregated or clumped spatial pattern, generating aggregated CWD within the forest stands (Harmon et al. 1986).

In addition to the variations in the CWD input, the decomposition process also varies considerably depending on several factors such as temperature, moisture, tree species, the diameter of CWD, the position of the log in relation to the ground and the decayer composition (Harmon et al. 1986), causing in the long run heterogeneity in the CWD volume and quality within and between the forest stands. As discussed before, the few exact measurements of decay rates in Fennoscandia show considerable variation in the decay rates of spruce between southern and northern boreal zones (Liu and Hytteborn 1991, Hofgaard 1993).

3.1.2. Effects of forest regeneration on coarse woody debris

The effects of logging on CWD volume and quality varied according to the regeneration method and the time since logging (I, V). The absolute CWD volumes varied from 8 m^3 ha^{-1} in the clear-cuts to 31 m^3 ha^{-1} in the 2-year old selective cuttings (I). The total volume of CWD was reduced by 60 % at the clear-cut sites compared with the total volume of old-growth spruce forests (I). In seed-tree cutting, the volume of CWD increased after logging compared with the pre-logging situation but at the 15-year old sites, the volume was at the level of old-growth forests (I). In the new type of selective

logging (2-year-old selectively logged sites), where some trees of all age classes were removed, the total volume of CWD remained at the level of the control sites (I) but was reduced by 40 % in old type of selective loggings, where only the largest trees had been logged (V). The main changes in the quality of CWD in all the regeneration methods were the remarkable reduces in the amount of snags and large-diameter logs (I, V).

The results on the volumes of CWD from managed forests in Finland are mainly available from the southern part of the country. In the national forestry inventory, the average CWD volumes in the managed forests of southern Finland varied from 1.2 to 2.9 m^3 ha^{-1} (Tomppo et al. 1998, 1999a, b, c). In general, the measured CWD volumes have shown variation according to the age of the stand, being 1.7 - 3 m^3 ha^{-1} in the stands under the age of 70 years, and 1.4 - 23 m^3 ha^{-1} in the older stands (see Siitonen 1998). In Sweden, the average CWD volumes in the national forest inventories were 3.5 m^3 ha^{-1} in the hemiboreal zone, but they were considerably higher, 9.7 m^3 ha^{-1}, in the northern boreal zone (Fridman and Waldheim 2000). However, low volumes have also been measured in managed forests of the middle and northern boreal zones of Sweden in individual studies, where the volumes varied from 1.7 - 2.3 m^3 ha^{-1} (Lämås and Fries 1995, Kryus et al. 1999). Siitonen (2001) estimates that the CWD volumes in the managed forests have decreased 92-98 % in the southern and middle boreal forests in Finland, and about 90 % in the northern boreal forest compared with old-growth forests. The low volumes of CWD recorded in the managed forests in central and southern Finland are related to the fact that most of the managed forests have been harvested at least twice since the first regeneration cutting, and the CWD volumes have been reduced in each harvest. In this study, the residual CWD from pre-logging was still clearly visible at the regeneration sites of timberline forests, contributing to the total volume of CWD (I, IV). In the timberline, the time since regeneration cutting was relatively short, and, besides residual CWD, larger-diameter logging waste also contributed to the total CWD volume. In the mesic spruce forests of northern Kainuu the decomposition rate is more rapid than in timberline forests, and the time since logging was longer. It is possible that some residual CWD still existed in these forests in the most advanced decay stage, even though this could not be detected since the logs in decay stage 5 were covered by a moss layer. No traces of logging waste were visible in Kainuu, except for the cut stumps (V).

There was considerable variation in the volume of CWD among the recently seed-tree cut sites. The increase in the mean volume was mainly caused by the volume of unmerchantable rotten butts, which were left on the ground during harvesting at some sites (I). At the recently logged seed-tree cut sites, the volume of snags was 16 % of the volume in pristine forests, but only 2-7 % at the older cutting sites. The proportion of large-diameter logs was one fourth of the respective volume of pristine forests at the recently logged sites, and 7 % at the older (15 and 40-year old) sites (I). The differences probably reflect the new forest management guidelines, which recommend leaving snags and decaying logs in the forest. The continuity of CWD formation was almost totally interrupted at the older seed-tree cut sites; the yearly input of new CWD in 40-year old stands being only 0.6 % of the respective volume in pristine forests (I).

After logging, the volume of CWD starts to decline gradually as a result of decomposition. The small-diameter logging waste had mostly disappeared in 15 years, but the decline in the total CWD volume between 1, 15, and 40-year old sites was rather small, indicating that the decomposition of larger logs is slow (I). In general, the successional curve of CWD after logging is "U"-shaped (Harmon et al. 1986). Both the residual CWD from the pre-logging period (predisturbance CWD) and the logging waste created in logging operations (disturbance CWD) contribute a relatively large amount of CWD after logging. In the course of time, both predisturbance and disturbance CWD decompose gradually, causing the U-shape in the middle of the successional period until the new growth of the forest stand starts to give postdisturbance input to the CWD volume. In North American hardwood forests, the highest amounts of CWD were observed in very old stands and in 10-year-old stands after clear-cutting. The lowest amount of CWD occurred 40-57 years after clear-cutting (Tritton 1980). The pattern was also observed in the managed sub-xeric forests of northern Karelia (Uotila et al. 2001). The seed-tree cut areas of timberline forests basically showed a similar pattern. It seems, however, that the U-shape is more gentle in seed-tree cut timberline forests: first, because the decomposition rate of large diameter CWD is very slow (I, IV) and, secondly, because it takes a long time before the new tree generation produces CWD of large dimensions. The mean diameter (DBH = 1.3 m) of trees in 40-year old stands in the timberline pine forests in Finnish Lapland is 7 cm, in 100 year old stands 12 cm, and in 200 year old stands 18 cm (Gustavssen and Timonen 1999). In this study, the average age of dominant trees in old-growth pine forests was

220 years, and the mean diameter 27.1 cm. Thus, it takes about 200 years before the pine stands in the timberline forests in Finnish Lapland start to produce large-diameter trunks.

Of all the studied harvesting methods, the volumes of CWD were clearly lowest at clear-cut sites. The low volume of CWD 15 years after logging is presumably a consequence of both efficient harvesting, the relatively rapid decomposition of the small-diameter logging waste of spruce, and soil preparation (ploughing) which may have destroyed part of the CWD. The volume of snags was 7 % of the respective volume found in old-growth spruce forests. These snags consisted mainly of birch. There were, however, spruce logs from the preharvesting time. The total volume of logs was 50 % and the volume of large-diameter logs (DBH > 30 cm) 15 % of the respective volumes in pristine forests (I). The decomposition of spruce is more rapid than pine (Esseen et al. 1992). This, together with the low volume of CWD after logging, makes the decline of the successional curve of CWD fairly steep after disturbance. The mortality of saplings had contributed to some new CWD at the sites. However, the slow growth of the pine planted at the sites makes the accumulation of new CWD very slow, and creates a gentle slope at the other end of the 'U-curve'.

The comparison of the effects of the two different selective logging methods is complicated because of the different time scales since loggings. The influence of the old type selective logging, which was directed to the largest trees in the stands, was still visible in the composition of CWD: the total volume of CWD was 40 % lower, the total volume of logs 56 % lower, and the volume of large-diameter logs (DBH > 30 cm) 40 % lower compared with the control sites (V). During the long time since logging some new CWD, mainly small-diameter logs and snags, have inevitably been recruited to the sites. However, the volume of decay stage 1 at the old selectively logged sites was only one third of the respective volume of the control sites, showing that forest structure and CWD input had not recovered to the level of pristine forests in 60-100 years (V).

In the new type of selective logging the volume was about at the level of control plots (I), but it has to be noted that the logging waste still contributed to the total volume of CWD (I). The volumes of large-diameter logs and snags were reduced also in the new type of selective logging (I). However, the volume of decay stage 1 was at the level of the control plots, indicating continuation in the supply of CWD. In the new type of selective logging, trees of all age classes are left in the forest. The uneven age structure

of trees permits the continuous availability of snags and logs of different sizes, which provides better circumstances for saproxylic organisms than other regeneration methods.

3.2. Forest structure and composition of beetle species

3.2.1. Beetle diversity in old-growth forests

The beetle species composition of timberline pine forests was studied in two successive summers. A total of 195 species (4905 individuals from 12 sites) was trapped in 1992 (I). Of the 89 species caught in Enontekiö Lapland (area 1, see Fig. 1), 43 species (48 %) were new to the province. Respectively, of the 174 species caught in Inari Lapland (areas 2,3 and 5) 44 (25 %) were new to the province, showing that the beetle fauna of timberline forests in Finnish Lapland has been poorly known (I). The species richness in the pine forests did not differ significantly among the study areas. Instead, there were differences in the species compositions. Both Renkonen's percentage index and Sørensen's binary index showed that the species compositions differed more between the geographically distant areas than between the nearer areas. The difference was more clearly demonstrated by Renkonen's index, which takes account both species richness and abundance, than by Sørensen's index, which takes account only the presence / absence of species (I).

In 1993, a total of 177 species (5751 individuals from 9 sites) were caught in pine forests, with 66 new species compared with the previous summer. The 34 % increase in the species number in 1993 indicates that a relatively high trapping effort is needed to obtain a comprehensive view of forest beetle fauna. The total number of species in the pooled catch of the two summers in the pine forests was 261. The ten most abundant species in the pooled catch comprised 66 % of all the the individuals (cf. II, Appendix, and III, Appendix), while 30 % were represented by only one individual. This supports earlier observations that in harsh and species-poor environments the species distribution follows geometric or logarithmic series, in which few species are dominant and the rest are relatively rare (Whittaker 1972, Magurran 1988).

Of the eleven rare species (less than 25 records in Finland in 1960-1990, see Rassi 1993) caught in the old-growth pine forests in 1992, all had northern

distribution (I). In 1993, the number of rare species trapped from the old-growth pine forests was six, with *Nephus bisignatus* (Boheman) being the only same species as in 1992. Of the species caught in 1993, *Oxypoda hansseni* Strand and *Thymalus subtilis* Reitter are northern in their distribution, while the others (*Ischnoglossa prolixa* (Gravenhorst), *Microdota palleola* (Erichson) and *Euplectus fauveli* (Guillebau)) have also been recorded in the southern parts of Fennoscandia. The rarity of some species with northern distribution, for instance *Nephus bisignatus*, which was trapped at several localities in two summers, may reflect the fact that northern areas are poorly studied instead of the rarity of these species.

In the study conducted in three different forest site types in 1993, a total of 299 species were trapped from the old-growth forests (III). Coarse woody debris was found to be an important factor contributing to the species richness of flying beetles in boreal timberline forests. 54 % of the species and 39 % of the individuals caught from the old-growth forests in 1993 were saproxylics (III). Higher proportions of saproxylic beetles have been recorded for hemiboreal spruce forests in southern Norway, where saproxylics comprised 67 % of the species in window flight trapping (Stokland 1994), whereas somewhat lower proportions have been recorded in the middle-southern boreal transition zone in southern Finland, where the proportion of saproxylic species was 42 % and proportion of saproxylic individuals 47 % in the spruce forests comprising both old-growth stands, and mature and over-mature managed stands (Martikainen et al. 2000).

The species richness of beetles followed the fertility gradient for the forest type. Both the rarefied total species richness and the rarefied species richness of non-saproxylic species were significantly higher in the mixed forests than in the pine forests. The difference in the species richness of saproxylics was not statistically significant due to the large variation in the species richness among the sites. Since the number of saproxylic species correlated with the total volume of CWD on the sites, the relatively high CWD volumes, and consequently the high number of saproxylic species found in some of the pine-dominated sites, affected the result, even though the mean number of saproxylic species per site was clearly higher in the mixed than it was in the pine forests**.**

In the correlation analysis, the main environmental factors contributing to the species richness of beetles were site productivity (as expressed by the number of vascular plants, the cover of eutrophic plants and thickness of humus layer), tree species composition, and the total volume of CWD and

the decay stages 3 and 4 (III). All these factors are strongly intercorrelated. Site productivity affects the volume of living timber, which in turn correlates with the volume of CWD (I). Tree species composition is also related to site fertility, the poorest sites in our study area being dominated by pine and the more fertile ones by spruce and deciduous trees.

Both the volumes of spruce and deciduous CWD correlated positively with the total species richness, and the latter with also the number of saproxylic species (III). Spruce and deciduous trees have been reported to host more invertebrate species than pine (Esseen et al. 1992, Rassi et al. 1992). According to Esseen et al. (1992), the higher invertebrate diversity in spruce is due to the more rapid decay process and more diverse fungal flora in spruce than in pine, which creates microhabitats for fungus-living species. Deciduous trees, especially aspen, host a large number of invertebrates, including many rare and threatened beetles (see, for instance, Seppänen 1970, Siitonen and Martikainen 1994). The presence of polyporous fungi also contributes to the species diversity of saproxylic beetle species on deciduous CWD. For instance, one of the commonest polypores on birch, *Fomes fomentarius*, hosts at least six cisids species as well as other beetle species from the genera Anobidae and Tenebrionidae (Kaila et al. 1994, Økland 1995, Fossli and Andersen 1998, Rukke and Midtgaard 1998, Rukke 2000). The negative correlation with the volume of dead pines is evidently spurious and due to the fact that the total volume of CWD was on average lower in the pine forests than in the spruce and mixed forests.

The volumes of CWD in the mid and late decay stages (3 and 4) showed high positive correlations with the number of saproxylics. In boreal forests, the peak of beetle diversity occurs in dead spruce trunks 5-20 years after the death of a tree, corresponding approximately to CWD in decay stages 2 and 3. The beetle fauna of these decay stages comprise many cambial feeders, fungal consumers, and their associates (Esseen et al. 1992). Decay stages 3 and 4 host the highest diversity of species associated with wood-decomposing fungi and a large number of threatened saproxylic species (Esseen et al. 1992, Jonsell et al. 1998). Similar successional stages but with a longer duration of the phases can be found in pine trunks, where the highest numbers of rare and threatened species are found in logs from ten to 70-80 years after tree death (Ehnström and Walden 1986), corresponding decay stages 3 and 4 in this study.

The species composition of the old-growth pine-dominated sites differed distinctly from that of the spruce-dominated sites (spruce and mixed forests)

in the DCA-ordination (III). The spruce-dominated sites overlapped when the saproxylic species composition was studied, whereas in the ordination of non-saproxylic species these forest site types were more clearly separated from each other (III). The probable reason for this is the high variety in microsite heterogeneity in the mixed forests. The structural heterogeneity due to higher tree species diversity, richer undergrowth vegetation, a more diverse litter composition, and better soil quality together with a thicker humus layer probably provide more favourable conditions for non-saproxylic fauna in the mixed forests compared with mesic spruce forests.

A total of 21 nationally rare species were trapped from the old-growth forests, and 14 of them occurred exclusively in the old-growth forests (III). Fifteen species were saproxylics and six non-saproxylics. The proportion of rare saproxylic species was clearly higher in spruce forests than in the other forest types. Two of the rare saproxylic species are included in the red data book of Finland: *Agathidium pallidum*, which was caught in a mixed forest, and *Pytho abieticola*, which was trapped in a spruce forest. Both species have declined as a result of the decrease of old-growth forests (Rassi et al. 1992).

3.2.2. Effects of seed-tree and clear-cutting on beetle fauna

The pooled data of old-growth pine forests and seed-tree cut sites comprised 258 species. The rarefied total species richness was significantly higher at the 1-year-old seed tree cut sites than in the old-growth pine forests, whereas there was no difference between old-growth forests and 15-year-old seed-tree cut sites (III). However, when the saproxylics and non-saproxylics were analysed separately, there was a significantly higher number of non-saproxylic species in the 15-year-old stands, while no differences were found in the numbers of saproxylic species. This seemingly contradictory result is due to the changes in species richness and composition in the course of time and in the variation in the species richness among the sites. Soon after logging the number of primary colonisers of CWD, which are attracted by logging waste, increases at the sites (Nuorteva 1956, Väisänen et al. 1993). In our data, many scolytids, curculionids and cerambycids, which were not found in the old-growth forests, were trapped on the seed-tree cut sites (III). At the same time, changes in climatic factors and undergrowth vegetation contribute to the increase in the number of many non-saproxylic species, e.g., species preferring open habitats and young successional stages. Thus,

the increase in the number of both saproxylics and non-saproxylics contributed to the increase of total species richness at the 1-year-old seed-tree cut sites. When logging waste starts to decompose gradually and there is no newly fallen CWD available, the number of cambial feeders and other primary stage saproxylics decreases (Esseen et al. 1992). In our data, the mean number of saproxylics was slightly lower at the 15-year-old sites than at the recently cut sites, which contributed to the total species richness. Although the rarefied number of saproxylics was higher at the 1-year-old seed-tree cut sites than in the old-growth forests, the difference was not statistically significant due to the large variation in species richness among the logged sites. The number of non-saproxylics, on contrary, remained high at the 15-year-old sites, showing significant difference to the old-growth forests (III).

The pooled species number of old-growth spruce forest and clear-cut sites was 216. No significant differences were detected in the rarefied species richness between the old-growth and regeneration sites. However, both the correspondence analysis and the species list revealed considerable differences in the species composition between the old-growth spruce forests and clear-cut sites (III).

None of the environmental variables showed significant correlation with the species richness of beetles in the regeneration areas, even though the volume of CWD in the decay stage 2 showed a high positive correlation with the number of saproxylic species ($r = 0.867$) and with the total species richness ($r = 0.870$). In the DCA ordination of saproxylic species, the openness gradient, characterized by the volume of stumps and branches, decay stage 1, and the cover of shrubs, separated the regeneration sites from the old-growth stands (III). In saproxylic species, the managed and old-growth stands were clearly separated from each other in both pine-dominated and spruce-dominated stands. In the DCA ordination of non-saproxylics the main environmental factors separating the regeneration sites and the old-growth stands were the cover of shrubs and mesotrophic plants. There was considerable overlap of the seed-tree cut sites and old-growth pine forests, indicating large similarity in the species compositions of non-saproxylics within the pine-dominated stands. The clear-cuts, on the contrary, were clearly separated from the old-growth spruce forests also in the analysis of non-saproxylic species.

Many changes in the species compositions due to logging were common to both seed-tree and clear-cut sites, but seemed to be more pronounced at

the clear-cut sites (III). In general, the responses of beetle species to logging can be summarized as follows:

(1) 37 % of the abundant species (min. 10 individuals in the pooled catch) were found in all the forest site types and regeneration areas. However, only five species (*Anthophagus omalinus*, *Malthodes guttifer*, *Eanus costalis*, *Liotrichus affinis* and *Anaspis arctica*) seemed to be relatively unaffected by logging, occurring relatively abundantly at all the study sites (the mean number per site at least five individuals in each forest category) (III).
(2) Species which are primary colonisers of CWD, such as cambial feeders and many of their associate species were favoured by the logging waste, and increased in number and abundance at the recently logged sites. Some of the species, such as *Acanthocinus aedilis* and *Asemum striatum* occurred only at the recently logged sites, while others, for instance *Hylastes brunneus*, *Tomicus piniperda* and *Hylobius abietis* were increased in numbers when compared to old-growth forests (III).
(3) Species that prefer open habitats or young successional stages increased in the logged areas. These included, for instance, species that feed on flowers as adults (*Judolia sexmaculata*, *Trichius fasciatus*), many elaterids developing in soil as larvae (*Orithalis serraticornis*, *Selatosomus melancholicus*, *Sericus brunneus*) and several saproxylic species that evidently favour decaying wood in open conditions (*Anaspis bohemica*, *Xylita laevigata*, *Ampedus nigrinus* and *A. tristis*) (III).
(4) A relatively large number of beetles in old-growth pine forests were also trapped at the seed-tree cut sites. This may be due to the fact that the old-growth pine forests near the timberline are naturally open even before cutting, and the environmental change from an old-growth to a seed-tree cut stand is relatively small. However, the dispersal of species and the edge effect may also contribute to the high species richness at seed-tree cut sites. Many groups of forest arthropods disperse actively into open young stands (Niemelä et al. 1996), and forest specialists may regularly colonise the open areas that are small islands in a landscape comprised mainly of older age classes (Spence et al. 1996). The forests surrounding our regeneration sites were mainly old-growth forests, which probably act as sources of colonisers for the regeneration areas. In addition, the mean size of 1-year-old seed-tree cut sites was only about 10 ha. In such small patches, most of the cut area may represent more an edge habitat than an open stand for many flying invertebrates. Forest

edges have found to be favourable habitats for many invertebrates that prefer or tolerate sun-exposed sites and shrub vegetation (cf. Helle and Muona 1985, Jokimäki et al. 1998).

(5) Species that are dependent on different microfungi were most affected by logging. Two very abundant saproxylic species in old-growth forests, *Hylecoetus dermestoides* and *H. flabellicornis*, were absent or occurred in low numbers at the logged sites; both species breed on recently dead trees and depend on ambrosia fungi. *Epuraea* spp. occurred in low numbers (both the number of species and abundance of individual species), or they were absent from the regeneration sites. Several cryptophagid and latridiid species in genera *Atomaria*, *Caenoscelis*, *Corticaria* and *Enicmus* similarly decreased at the seed-tree cut sites and had practically disappeared from the clear-cut sites (III). All these species are mycetophagous and are known or supposed to depend on different kinds of "microfungi" (molds, fungi imperfecti, Myxomycetes etc.). These changes are most probably related to the changes in microclimate, since most microfungi are sensitive to drought.

(6) Unlike most other fungivorous species, the number of species and abundance of some cisids, which live in polyporous fungi, increased at the 15-year-old seed-tree cut sites (III). This is explained by the relatively high number of species and basidiocarps of polyporous fungi that was detected at these sites mainly due to the favourable decay stage of logging waste (IV).

(7) The proportion of rare saproxylic species was higher at the recently seed-tree cut sites (8 % of the total species number of the forest type) but lower at the 15-year old seed-tree cut sites (2.5 %) when compared with the old-growth pine forests (4.3 %). In the clear-cuts, the proportion of rare saproxylic species was distinctly lower (1.2 %) than in the old-growth spruce forests (11.2 %) (III). These differences are probably the result of changes in the CWD quality, disrupted recruitment of CWD at the older sites, and the microclimatic changes caused by logging. As shown by Kaila et al. (1997), there are rather strict habitat specialists both among the rare species that inhabit open, sun-exposed habitats, and among those preferring closed forests. It is probable that the recently seed-tree cut areas provide habitats for the former group. Evidently, both the lack of suitable substrate and the changes in microclimate affect the low species numbers of rare saproxylics at the 15-year-old regeneration sites.

(8) The species composition of 15-year old clear-cut of spruce forest sites, which had been planted with pine, was in transition. Many of the characteristic species of old-growth spruce forests were absent or less abundant in the clear-cuts. The two most dominating scolytids in old-growth spruce forest, *Hylastes cunicularius* and *Hylurgops glabratus*, had practically disappeared from the clear-cut sites. A number of species confined to pine had appeared at the sites. These included *Dasytes obscurus*, which is a predatory species on pine saplings, and species living in phloem of freshly dead trees (*Magdalis phlegmatica*, scolytids *Pityogenes bidentatus*, *P. lichtensteinii* and *Tomicus piniperda*) (III). With the replacement of main tree species, the beetle communities of spruce forests will gradually shift into communities of pine forests. Studies on some arthropod groups show that the recovery of their populations has taken 60-80 years after clear-cutting (J. Niemelä 1999). In this case, the transition probably lasts more than a century because of the change of the main tree species. The landscape level location of source areas (pine forests) contributes to the colonisation time and species composition and it is possible that species with poor dispersal ability will remain absent from the sites.

Similar kind of results as described above were observed among ground-living carabids by Niemelä et al. (1988, 1993), who distinguished three different groups of species in their responses to clear-cutting: 1) forest generalists which were not dramatically affected by logging, 2) species of open habitats which increased in abundance, and 3) mature forest species which disappeared or decreased in abundance. However, species trapped by window flight traps form an ecologically more mixed lot, showing more diversity in their responses than carabids, which are mainly ground-living predators.

The responses of saproxylic beetles to forest regeneration varied according to the habitat requirements and dispersal ability of a species. In this study, five groups of saproxylic beetles could be distinguished according to their habitat requirements and their relations to substrate availability:

(1) Species that breed and feed on recently died trees or CWD. These species increased in number and abundance at the young regeneration sites (III), and evidently both the regeneration cutting and the subsequent forest management practices that create logging waste (removal of seed-trees and thinning) provide suitable substrate for these species. In general,

primary colonizers such as bark beetles and bark weevils have good dispersal ability, and they can locate suitable substrate from a long distance (Solbreck 1980, Nilssen 1984), which enables their survival in managed forests and over wide landscape areas.

(2) Species that prefer or are able to inhabit CWD in open conditions and which are not very restricted in their substrate requirements. In this data, species inhabiting CWD in open conditions increased in number at the logged sites (III). These species can evidently thrive in regeneration areas, provided that the substrate availability and continuity are ensured. However, the paucity of substrate and the low recruitment of new CWD in both seed- tree and clear-cut stands (I) may cause a decline of these species in the course of time.

(3) Species that are specialized in their substrate requirements but which are not very sensitive to microclimate changes. An example of these are some cisid species, which were trapped at the logged sites (III). Like the previous group, also these species could in principle survive in regeneration areas, but he disruption in CWD continuity in the old regeneration areas may cause decline of populations and local extinctions of many of these species. The survival of cisids, for instance, is tied on the survival and fruit-body production of the polyporous fungi where these species are living in.

(4) Species which live on fungi that are sensitive to microclimatic changes. Many relatively common fungus-living saproxylics of old-growth forests were decreased or absent in the clear-cuts (III). Even though there is no direct evidence, it seems probable that their decline is related to the changes in microclimate, which affects their substrate. Populations of these species may be difficult to maintain in the regeneration areas.

(5) Species that are confined to moist, shady environment and are often specialized in their CWD requirements. These species require long forest continuity, and seem to be sensitive to microclimatic changes. For instance, *Pytho abieticola*, a rare species which was trapped in spruce-dominated old-growth stand (III) is known to inhabit old-growth spruce forests which have long forest continuity (Rassi et al. 1986). Decline of these kind of species has been obvious in the managed forests in Finland during the past decades (Rassi et al. 1992, Mannerkoski 1996, Punttila 2000). Preserving populations of these species may turn out to be difficult or impossible in the regeneration areas.

The results indicate that several groups of saproxylic beetles are able to live in regeneration areas, provided that suitable substrate is available. Similar results have been obtained by Martikainen (2000), who found that a large portion of saproxylic species may survive in open conditions. However, it has to be noted that the 15-year time span of the present study is a relatively short period, and many changes in the composition of saproxylic species can be delayed because of the slow decay process in northern latitudes. Thus, the possible loss of some species may be detectable only in the long run ("extinction debt", see, e.g., Tilman et al. 1994, Hanski 2000). On the basis of the low recruitment of new CWD, it seems probable that in many older regeneration areas lack of substrate continuity will lead to local extinctions of also those species, which could otherwise inhabit managed forests.

Leaving retention trees of different tree species and trunk sizes may provide suitable habitats for those saproxylic beetles that are not sensitive to microclimatic changes. However, it may turn out to be difficult or impossible to maintain in regeneration areas populations of those species which are restricted in their microclimate adaptations to moist and shady environment.

3.3. Wood-decomposing fungi

3.3.1. Species diversity in old-growth pine forests

The total number of lignicolous fungi recorded in the old-growth and managed pine forests near the timberline was 47; of these, 24 polypores were recorded on pine (IV). The total number of species found in old-growth pine forests was 31. Of these, 14 were polypores recorded on pine, eight polypores on deciduous CWD, and nine were corticoid species. Relatively few comprehensive studies have been conducted on the polypore flora of the pine forests in the northern boreal zone. Renvall (1995) recorded 32 polypores on pine trunks in his large-scale study of wood-inhabiting fungi in northeastern Lapland near the timberline. The total number of species recorded on pine in this study represents about 75 % of the species found on pine in these latitudes, and the number of species recorded in old-growth forests about half of the probable total species richness.

There was a large variation both in the species number (10-22) and in the number of records (18-109) among the old-growth forest sites (IV). This variation can be a result of several reasons, such as due to the differences in the quantity and quality of CWD, differences in stand histories, the different dispersal abilities of species, and interspecific competition. In general, there was a positive correlation between the volume of CWD and the numbers of species and records at the sites (IV). The differences in the stand productivity partly explain the differences in the species number between the Nukkumajoki and Sotajoki sites (20 vs. 13 species), because the two sites in Sotajoki area were poorer in timber production (the volumes of living timber 42.4 and 60.2 m^3 ha^{-1}) than the sites in Nukkumajoki (83.9 and 104.2 m^3 ha^{-1}), and, respectively, the volumes of CWD were much lower in Sotajoki area (9.4 and 7.2 m^3 ha^{-1}) compared with volumes in Nukkumajoki (17.1 and 32.3 m^3 ha^{-1}).

Even though the total number of species recorded in the old-growth pine forests was low, the diversity indices at old-growth sites were high. The alpha diversity index was the highest at the site where only 18 records were made, these, however, belonged to ten different species. Strikingly dominant species were lacking from old-growth forests. The majority of species (86 %) were species inhabiting mid or late decay stages of CWD, while the proportion of pioneer species was 14 % (IV). The numbers of records followed the same pattern. The relatively low proportion of pioneer decayers in the old-growth forests is due to the low yearly input of CWD (I), but it is also due to the fact that the newly fallen CWD hosts a relatively low number of species (Renvall 1995). The mid and late stages of CWD generally host the highest diversity of wood-inhabiting fungi (Bader et al. 1995, Renvall 1995, Høiland and Bendiksen 1997). This was also clearly visible in this data: of the 31 species recorded in old-growth forests, 27 occurred on CWD beloning to decay stages 3 or 4 (IV).

Of the different CWD qualities, the highest number of species (24) and records (74 % of all the records) were found on logs (IV). Seven species (18 % of records) were found on natural stumps, and six species (8 % of records) on snags. The relatively high proportion of records on stumps was due to the records of *Piloderma croceum*, which is a mycorrhizal fungus and was mainly found on old, well-decayed stumps.

The presence of deciduous trees considerably increased the species richness of wood-decomposing fungi in pine forests. A total of eight species living on deciduous CWD contributed 26 % to the total species richness

recorded in the old-growth pine forests. Polypores on both deciduous and coniferous CWD host numerous invertebrates, thus contributing also to their diversity boreal forests (see, e.g., Kaila et al. 1994, Økland 1995, Fossli and Andersen 1998, Rukke and Midtgaard 1998, Rukke 2000, Komonen et al. 2000).

Many wood-decomposing fungi are commonly used as indicators for the conservation value of forest stands. Kotiranta and Niemelä (1996) distinguished two groups of indicator species: old-growth forest indicators and virgin forest indicators. According to Kotiranta and Niemelä (1996), old-growth forest indicators prefer old, naturally regenerated forest stands with large-diameter trees. Some of these species can be found occasionally in a manmade environment or in forests with slight loggings, but when growing in natural environment they prefer forests with old tree individuals and a large amount of logs in mid or late successional stages. Virgin forest indicators clearly prefer the oldest coniferous forests with no trace of human influence. Many virgin forest indicators live on very large-diameter old logs, and some of them grow only on the CWD inhabited earlier by a certain fungus species. Both indicator groups include species that are classified as threatened in Finland (Kotiranta and Niemelä 1996).

Altogether, nine old-growth forest indicator species were found in the old-growth timberline pine forests. Of these, *Chaetodermella luna* (13 records) and *Oligoporus sericeomollis* (21 records) were relatively abundant, while the records of other species (*Asterodon ferruginosus, Gloeoporus taxicola, Junghuhnia luteoalba, Odonticium romellii, Phellinus nigrolimitatus, Phellinus viticola* and *Postia lateritia*) varied from one to four (IV). Of the four virgin forest indicators, *Skeletocutis jelicii* was found only once, while the records of other species (*Antrodia albobrunnea, Postia hibernica* and *Skeletocutis lenis*) varied from 3 to 8 (IV). The proportion of indicator species was very high in some of the stands: at a site where only ten wood-decomposing fungi were recorded, nine of them were old-growth and virgin forest species (IV), probably indicating a long substrate continuity in these stands.

Five threatened species were recorded: *Antrodia albobrunnea*, *Postia hibernica*, *Postia lateritia*, *Skeletocutis lenis* and *Skeletocutis jelicii* (IV). Of these, *P. hibernica* and *P. lateritia* were growing on relatively thin CWD (14-16 cm), while *S. lenis* and *S. jelicii* clearly preferred thicker trunks (23-34 cm) (IV). All these species grew on CWD in mid or late decomposition stages. *Postia hibernica*, *Postia lateritia,* and *Skeletocutis jelicii* were mainly found on decay stage 3, while *Antrodia albobrunnea* and *Skeletocutis lenis* were most frequently found on decay

stage 4. Similar results were obtained by Renvall (1995), who found that *Postia hibernica* and *P. lateritia* were frequent on decay stage 3, while the strongly decayed pine trunks (decay stage 4) were characterized by the presence of *Antrodia albobrunnea* and *Skeletocutis lenis.*

3.3.2. Species diversity in old-growth spruce forests

The total number of species recorded in old-growth and selectively logged spruce forests in Kainuu was 68 (1384 records) (V). Of these, 63 species (922 records) were found in old-growth forests. The species numbers at individual sites varied from 24 to 34; the lowest record was at the site that had one data set less than the other sites (V). The total number of species in the Metsäkylä area was 42, and in the Paljakka area 48. In the earlier inventories of the old-growth, spruce-dominated, mixed forests in Kainuu the numbers of polypore species varied from 43 up to 79 in different areas (Penttilä 1994). The methods of the different studies are not, however, directly comparable. If the species numbers of this study (42 and 48), which included one inventory day per site in each area in two successive summers, are compared with the cumulative species numbers of two inventory days per area in Penttilä's research (34-52 species), the variation in the species richness found in our study areas fall within the range of other old-growth forests in Kainuu.

Altogether, 41 polypore species were growing on spruce. Somewhat lower number of species has been recorded on spruce near the timberline (36, Renvall 1995), indicating that the species richness of polypores remains relatively high within the northern boreal zone up to the timberline. The commonest species on spruce were *Trichaptum abietinum, Phellinus viticola,* and *Fomitopsis pinicola* (V). Many of the common polypores are of importance to the beetle diversity in boreal forests. For instance, *Trichaptum abietinum* and *Fomitopsis pinicola* have been reported to host particularly diverse beetle fauna (Esseen at al. 1997), as has *Fomes fomentarius* (see chapters 3.2.1. and 3.3.1), which was the commonest species on deciduous CWD.

Of the recorded species, 24 were growing on deciduous CWD. Deciduous trees contributed relatively more to the species diversity of polyporous fungi in spruce forests (38 % of species) than in pine forests (26 %). This is due to a more diverse tree species composition of spruce-dominated stands. In addition to birch, especially the presence of aspen increased the diversity of

polypores, due to many species confined exclusively (e.g., *Phellinus populicola*, *P. tremulae*, *Inocutis rheades*, *Rigidoporus corticola*) or facultatively (*Ganoderma lipsiense*, *Postia alni*) to aspen.

Of the 63 species, 60 were recorded growing on logs, 21 on snags, 13 on branches, and 5 on natural stumps (V). Like in timberline pine forests, the majority of records were made on logs (79 %). The proportions of records on snags were 15 %, on branches 4 % and on stumps 2 % (V). Decay stage 3 hosted the highest number of species (54) and records (457). The species richness was also high in decay stages 2 and 4 (29 and 31 species, respectively), whereas the species richness on both very fresh and well decayed CWD was low (5 and 4 species).

Altogether nine species, which are regarded as old-growth forest indicators (according to Kotiranta and Niemelä 1996), and five virgin forest indicators were recorded (V). Many of the old-growth forest indicators were very abundant, e.g., *Phellinus viticola* (148 records), *P. nigrolimitatus* (33) and *P. chrysoloma* (30), or relatively abundant like *Phellinus lundellii* (11) and *Fomitopsis rosea* (11) (V). Of the virgin forest indicators, *Amylocystis lapponica* was relatively abundant (12 records), whereas the others (*Antrodia albobrunnea*, *Diplomitoporus crustulinus*, *Junghuhnia collabens*, and *Skeletocutis stellae*) were presented only by one record. *Fomitopsis rosea*, *P. nigrolimitatus* and *Amylocystis lapponica* were found to be among the commonest polypores on fallen spruce trunks in the virgin forests in northeastern Lapland (Renvall 1995), and they were also among the 15 commonest species in the old-growth forests of Luosto in central Lapland (Niemelä and Dai 1999). All these three species also preferred relatively large-diameter CWD (31-46 cm)(V).

Among the other indicators species, *Phellinus viticola*, *Junghuhnia collabens*, *Leptoporus mollis*, and *Diplomitoporus crustulinus* were growing on relatively thin CWD (11-15 cm). With the exception of *Diplomitoporus crustulinus*, *Leptoporus mollis*, *Junghuhnia collabens* and *Phellinus chrysoloma*, which were growing mainly on CWD at decay stage 2, all the other indicators preferred mid or advanced decay stages.

Six of the indicator species are considered as threatened in Finland (V). *A. albobrunnea* typically grows on old, well-decayed pine trunks (Renvall 1995), and it was recorded on large-diameter pine trunk. Both records of *Postia lateritia*, which mainly grows on pine (Renvall 1992), were made on relative small-diameter spruce trunks. Both *Skeletocutis* species (*S. odora* and *S. stellae*) were recorded on mid-diameter logs, and, as mentioned above, *Diplomitoporus crustulinus* and *Junghuhnia collabens* on relatively thin CWD.

3.3.3. Effects of seed-tree cutting on polypore diversity of pine forests

A total of 37 lignicolous fungi were recorded at the seed-tree cut sites; of these, 26 were polypores. Altogether, 21 polypores were growing on pine and five on deciduous CWD. The number of species at individual sites varied from 13 to 20 (IV). Although the data are relatively small, the results show clear changes in the species compositions of polypores due to logging. The successional stages of logging waste were reflected in the species composition of wood-decomposing fungi throughout the sites of different ages after logging. The proportion of pioneer species increased rapidly at the recently logged sites, and at 3-year old sites, 60-75 % of the records were made on logging waste. The great majority (75 %) of these records was composed of the two commonest pioneer decayers: *Stereum sanguinolentum* and *Phlebiopsis gigantea*. At the 18-year-old sites, the proportion of pioneer species had decreased to less than 10 % of the records, and the mid stage decayers prevailed. Both the number of species and the alpha diversity were relatively high at the 18-year old logging sites (IV), reflecting the fact that the majority of logging waste was at the stage suitable for mid-stage decomposers. At 42-year old logging sites, the pioneer species had disappeared from the logging waste, but some of them were found on dead saplings and young trees. The proportion of mid decayers was still high, but the proportion of species preferring advanced decay stages had declined to less than 20 % of the total species number, while their proportrion was over 40 % in old-growth forests (IV).

The species recorded showed different tolerance to logging. Based on this study, the logging waste was able to host at most half the species number of wood-decomposing fungi of old-growth pine forests. On the other hand, residual CWD from pre-logging time still maintained a large portion of the species of old-growth pine forests for several decades after regeneration cutting. Three different groups of wood-decomposing fungi in pine forests could be distinguished according to their habitat requirements and responses to logging:

(1) Pioneer species on dead wood. These species increased rapidly on the logging waste at the 3-year old logging sites but they were mainly absent from the older regeneration areas. However, some of them were recorded on dead saplings in the 42-year old stands, indicating that these species

have good dispersal ability. Relatively few studies have been conducted on the dispersal ability of wood-decomposing fungi. However, these studies show that aerial spore dispersal may vary considerable depending on the species (see Nordén 2000). The continuous input of CWD in the old-growth forests will maintain source populations of pioneer species, and successive management operations will occasionally provide suitable habitats for pioneer species in logging areas. Populations of these species are unlikely to become extinct at the stand level unless very wide landscapes are simultaneously treated by logging.

(2) Species that live on mid or relatively small-diameter CWD and are not very sensitive to microclimatic changes. Many of these species are classified as indicators of old-growth (*Chaetodermella luna, Oligoporus sericeomollis, Phellinus viticola, Postia lateritia, Junghuhnia luteoalba*) or virgin forests (*Antrodia albobrunnea, Postia hibernica, Phlebia cornea, Skeletocutis stellae*). These species seemed not to be very sensitive to environmental change caused by logging, and the fact that they thrived at the logged sites indicates that the occurrence of these species is mainly restricted by the availability of suitable substrate. Some of these species were also able to invade logging waste, showing a relatively wide ecological tolerance. Leaving mid-diameter CWD and retention trees on the regeneration stands may enhance the survival possibilities of these species in managed forests.

(3) Species that are restricted to their substrate requirements and which are possibly sensitive to microclimatic changes. These were mainly species preferring relatively large-diameter trunks in advanced decay stages. Indicator species recorded only on residual CWD included *Skeletocutis lenis, Odonticium romellii* and *Antrodia infirma*. The indicator species that were completely lacking from the logged sites were *Phellinus nigrolimitatus, Gloeoporus taxicola,* and *Skeletocutis jelicii*. All these species have also shown a narrow ecological tolerance in earlier studies (Bader et al. 1995, Renvall 1995). However, the roles of microclimate, dispersal ability, and interspecific competition for the establishment and survival of these species still need further studies. Maintaining viable populations of these species in managed forests seems difficult.

Based on this study, it seems probable that because of the low accumulation rate of new CWD at the seed-tree-cut sites, especially that of larger diameters (I), many species with specific habitat requirements may

die away from the managed sites in the course of time. The low decomposition rate of large-diameter residual CWD in pine-dominated timberline forests contributes to a long time lag (extinction debt) in the loss of species, which means that the effects of logging on the species diversity of wood-decomposing fungi can be detected only several decades or a century after logging.

3.3.4. Effects of selective cutting on polypore diversity of spruce forests

The selective logging of the spruce forests in northern Kainuu took place 60-100 years ago. The harvest was mainly directed at the largest trees in the stands. The intensity of logging varied greatly; the number of cut stumps varying from 26 to 211 per hectare (V).

Both the number of polypore species and the number of records were significantly higher in the primeval stands than in the selectively logged stands (63 species and 922 records in primeval forests versus 40 species and 462 records in the logged forests). The difference was found in the species inhabiting coniferous CWD, whereas no difference was observed in the species numbers on deciduous CWD (V). The volume of CWD in the early and mid decay stages was low at the logged sites, indicating that the CWD supply had not recovered to the level of pristine forests in 60-100 years. However, no differences were found in the species richness of polypores on the decay stages 1 and 2 between the old-growth and logged sites, which shows that a relatively low supply of CWD can maintain the diversity of primary decayers.

Both the volumes of large-diameter CWD and CWD in decay stage 3 were low in the selectively logged forests, representing 54 % and 43 % of the respective volumes of the old-growth stands. Although these differences were not statistically significant, they were large enough to cause a major decline in species richness. The species richness in decay stage 3 was significantly lower in the selectively logged stands than it was in the old-growth stands, as well as the species richness in the diameter class 20-29 cm. The species richness of the polypores found exclusively on large-diameter trunks (DBH >30 cm) was clearly higher in the old-growth forests (15 species) than at the logged sites (5 species) (V). Similar results have been obtained by Bader et al. (1995), who found that the log size in the selectively cut stands significantly influenced the total species number, the number of

threatened species, the number of species per log, and the hymenial surface area per log.

Not only the species richness but also the species composition was affected by logging. The primeval stands had a more homogenous species composition (the average percentage similarity 64.1 %, varying from 52-76 %) than the logged sites (51.1 %, varying from 29-75%). On the trunk level, the average number of species per trunk was significantly lower in the logged stands (1.14) than in the pristine stands (1.32). The proportion of trunks hosting three or more species per trunk was lower at the logged sites (3 % of all the logs) compared with pristine stands (6 % of all the logs) (IV). This may be a result of changes in interspecific competition within the trunks, so that a stronger coloniser can take over a patch from a weaker colonizer, or prevent a weaker coloniser from becoming established on the trunk (Rayner and Boddy 1988 a, Holmer 1996). It is also possible that the restricted dispersal ability of some species (see Penttilä et al. 1999) may reduce the occupancy of trunks at logged sites where the distance between suitable microhabitats can be long.

Likewise some indicator and threatened species in the logged pine forests, some indicators of old-growth or virgin spruce forests showed a surprisingly wide ecological tolerance. All the old-growth forest indicators belonging to the genus *Phellinus* (*P. viticola, P. chrysoloma, P. nigrolimitatus, P. lundellii, P. ferrugineofuscus*) were also found at the logged sites, some of them abundantly. Some of these species can live on a relatively dry wood (*P. viticola* and *P. lundellii*), but also species that are considered to be sensitive to environmental changes such as *P. nigrolimitatus* were recorded at the logged sites. It has to be noted, however, that the intensity of selective logging has varied considerably between and even within the stands, and suitable habitats may be preserved or emerged in some localities. On the contrary, *Fomitopsis rosea* and *Amylocystis lapponica*, which are relatively common in the old-growth spruce forests in northern boreal zone (Renvall 1995) were absent or occurred in low numbers at the logged sites. Similar results have been obtained by Bader et al. (1995) and Bredesen et al. (1997), who found that these species were mainly absent from managed forests. Both species seem to be very sensitive to environmental changes, and they also indicate well the large-diameter log continuity in spruce forests. *Phellinus ferrugineofuscus*, which is also used as an indicator of log continuity (see Karström 1992, 1993), seemed to be able to inhabit mid-diameter trunks, and some records of this species were made at selectively logged sites.

In these results, the effects of logging were more pronounced in the spruce-dominated than in the pine-dominated forests. The possible reasons, which probably all partly affect this result, are the differences in the sensitivity of the species to environmental changes, differences in logging methods, and the long time span since logging in the selectively cut stands. It is probable that some of the polypores in the spruce-dominated forests are adapted to closed, shady forests with stable microclimatic conditions, and they cannot adapt to the environmental change caused by logging. Selective logging was conducted in the large areas in northern and eastern Finland in a relatively short period, which led to interruption in the continuity of large-diameter trunks over wide areas. This may have caused the local extinctions of populations, with no source areas for recolonization. Finally, due to the long time since logging, the residual CWD from pre-logging time was decomposed and it could not maintain polypore populations like it still did at the seed-tree cut sites near the timberline.

Roughly similar groups to those in the pine-dominated stands could be distinguished among the polypores of spruce-dominated forests in relation to habitat requirements of species and their responses to logging:

(1) Forest generalist, many of which are pathogens or primary decayers. These include many of the commonest species on both spruce and deciduous trees, for instance *Trichaptum abietinum*, *Fomitopsis pinicola*, *Fomes fomentarius*, and *Phellinus cinereus*. These species were found abundantly both at the old-growth and the logged sites and, with substrate continuity, they will undoubtedly survive in the managed stands. Evidently, these species have relatively good dispersal ability. For instance, genetic studies on *Fomitopsis pinicola* suggest a high rate of gene flow over a wide area, even though there is no evidence of this by spore trapping (Nordén 1997).
(2) Old-growth forest indicators, which live on small or mid-diameter CWD, and which are not very sensitive to changes in microclimate. These included for instance above mentioned *Phellinus viticola* and *P. lundellii*, which can live on relatively dry CWD, and species that can live on a small-diameter CWD, such as *Diplomitoporus crustulinus* or *Skeletocutis lilacina*. These species would at least to some degree benefit of the retention trees left at the regeneration sites.
(3) Species that are restricted in their substrate requirements and which are sensitive to microclimatic changes. The best examples of species in this

category are *Fomitopsis rosea* and *Amylocystis lapponica*, both of which were mainly absent from the logged stands. The sensitivity of *F. rosea* to forest fragmentation has been demonstrated by Högberg (1998) and Komonen et al. (2000). Komonen et al. (2000) suggest that the primary reasons for its absence from small forest fragments are the lack of substrate and limited dispersal ability, but sensitivity to microclimatic changes and interspecific competition cannot be excluded as explanatory factors.

4. CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

The main results of this thesis, with some implications for practical forestry, can be summarized as follows:

(1) Coarse woody debris turned out to be an important component for biodiversity in old-growth northern boreal forests. Over half the beetle species in window flight trapping were saproxylics (III), and the diversity of polypore flora was high (IV, V). There was a large variation in the CWD volume within each forest site type (I, V), due to both local variation in timber productivity and the stochastic nature of disturbances. However, there was a yearly input of new CWD in the stands as a result of small-scale gap dynamics, which ensures CWD continuity within old-growth forests (I, V).
(2) The volume of CWD in old-growth stands was related to the volume of living timber, being highest in the most productive sites (I). Besides variation between the forest site types, which was related to productivity, both large- and small-size disturbances create variation within the stands (I, V). In order to better mimic the natural variability of CWD volumes, the number of retention trees and the amount of CWD left in the managed forests, should, instead of fixed amounts, vary both between and within the forest site types.
(3) The majority (60-80 %) of CWD in the old-growth forests was logs. The volume of large-diameter logs (DBH >30 cm) was up to 50 % of the total volume of CWD in the most productive stands, and 14-17 % in the poorer forest site types. The continuity of large-diameter logs turned out to be vitally important for many rare polypore species (IV, V).

The mid and late decay stages of CWD, which predominated in the old-growth forests, hosted the highest diversity of polypores (IV, V), and showed high positive correlation with beetle species richness (III). One fifth of CWD in the old-growth forests were snags (I), which are important for cavity-nesting birds (Samuelsson et al. 1994), and provide new logs in the course of time. The continuity of these CWD qualities could partly be ensured by leaving some large-diameter trees unlogged in all regeneration methods.

(4) Of the studied regeneration methods, the new type of selective cutting, where trees of all age and diameter classes remained in the forest, ensured best the continuity of CWD (I). The volume of newly created CWD was at the same level than in the old-growth forests, while all the other regeneration methods showed considerably lower volumes of newly created CWD (I, V). Old type of selective cuttings with the harvest of the largest trees of the stand showed lower total volumes of CWD than the control sites, and lowered input of new CWD (V). In seed-tree cutting, part of forest structure was retained in the form of seed-trees at the beginning of the regeneration period but after removal of seed trees, the formation of new CWD was low. Clear-cut areas had the lowest total volume of CWD and low recruitment rate of new decaying wood (I).

(5) The presence of deciduous trees considerably increased the diversity of beetles (III) and polyporous fungi (IV, V). In boreal forests, which are generally species-poor, the presence of birch as an admixture has a direct impact both on invertebrate and polypore diversity (III, IV). Other deciduous tree species, especially aspen, also increased the diversity of polypores (V).

(6) The results indicate that local extinctions of many saproxylic species are probable in the old regeneration areas, where little CWD and no retention trees have usually been left at the sites. The low number of polypores on the logging waste of seed-tree cut areas and the absence of many species confined to large-diameter CWD in advanced decay stages indicate that small-diameter logging waste is not able to maintain the full diversity of polypores (IV). Similarly, the significantly lower species richness of polypores at the old selectively logged sites shows that a reduction in the amount of large-diameter CWD may cause the local extinctions of species in the longer time perspective. The effects of this

extinction debt may be detectable only decades or over a century after logging.

(7) Both the beetle and polypore species of pine forests seemed to be less sensitive to logging than the species of spruce forests (III, IV, V). The species composition of non-saproxylic beetles showed great similarity between old-growth pine and seed-tree cut sites (III). Many polypores typical to old-growth pine forests still lived on the residual CWD from pre-logging several decades after seed-tree cutting, and some of the species were able to invade the logging waste (IV). Retention of some seed-trees in the stands may help these species to survive until the growing forest again starts to produce large-diameter CWD.

(8) Based on these results, the paucity of suitable substrate seems to be the primary reason for the absence of many saproxylic species from regeneration areas (III, IV, V). However, the results also indicate that many species, especially those of spruce forests, are sensitive to microclimatic changes (III, V). Restricted dispersal ability and interspecific competition are also among the factors that may limit the survival of saproxylics, and their role still needs further studies. The paucity of substrate in a stand level can be partly mitigated by leaving retention trees and CWD in logging areas. However, it is hard or impossible to mitigate the impacts of microclimatic changes or influence to species competition or restricted dispersal ability. For that reason, a network of protected areas is needed to maintain the full diversity of forest species in northern boreal forests.

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